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Woody Plant Communities of the Iowa Loess Hills: Expansion From 1855 to 2000, Extant Composition, and Ecological Succession.

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Woody Plant Communities of the Iowa Loess Hills:

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By

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Abstract

Woody Plant Communities of the Iowa Loess Hills:

Expansion From 1855 to 2000, Extant Composition, and Ecological Succession

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The Loess Hills of western Iowa are a unique geologic landform historically covered by scattered bur oaks in a matrix of mixed-grass prairie. Since European settlement, however, woody plant encroachment has altered the ecosystem and presently endangers the last substantial prairie remnants in Iowa. Aerial photographs from 2000 and General Land Office field survey notes from the 1850s documented an increase in woody plant cover from 7% in 1855 to 25% in 2000 for three counties in the Loess Hills region of western Iowa. Woody plant species composition along a lowland-ridge-top coenocline on both north and south aspects in centrally located Monona County, Iowa, was evaluated to quantify extant vegetation and to serve as a base for future comparison. Ridge-tops were dominated by smooth sumac (*Rhus glabra*), eastern red cedar (*Juniperus virginiana*), and rough-leaved dogwood (*Cornus drummondii*) with middle slopes dominated by bur oak (*Quercus macrocarpa*), ironwood (*Ostrya virginiana*), green ash (*Fraxinus pennsylvanica*), or hackberry (*Celtis occidentalis*). Lower slopes were dominated by American linden (*Tilia americana*) with an understory of ironwood,

although green ash and hackberry also were represented. Assuming woody plants expand upslope, these communities infer a sere for the study site succeeding from eastern red cedar to bur oak–ironwood to hackberry–ironwood communities on hilltops and slopes with species such as American linden, green ash, or hackberry dominating lower slopes. Overall, this study indicated that, in the absence of active management, woody communities of some type can ultimately be expected to replace both the prairie remnants of the Iowa Loess Hills and the extant bur oak-dominated forest.

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Table of Contents

List of Tables and Figures

Tables

Figures

Introduction

The Loess Hills of western Iowa constitute a unique 5-16 km wide geologic landform extending approximately 320 km through seven of Iowa's and two of Missouri's westernmost counties (Fig. 1). The western edge of this narrow band of rugged hills rises abruptly from the Missouri River floodplain, reaching up to 90 m in height, but grades to gently rolling hills to the east (Mutel 1989). The majority of the loess soil that underlies the Loess Hills was deposited during the Wisconsinan glacial stages near the end of the Pleistocene, approximately 31,000-12,000 YBP (Bettis *et al.* 1986). Since then, wind and water movement have carved the Loess Hills into what has been called one of Iowa's most unique physiographic areas (Bettis *et al.* 1986, Prior 1991).

Loess is a porous, eolian soil that drains well. This characteristic, as well as steep western slopes and the 659-888 mm of precipitation received each year (U.S. Dept. of Commerce 1973-1983), result in a xeric environment that supports disjunct mixed-grass plant communities more similar to those occurring in western portions of the Great Plains than to the tallgrass prairie in which this landform is embedded (Carter 1963, Novacek *et al.* 1985). The north-to-south orientation of the Loess Hills also results in a latitudinal climatic gradient with conditions being more xeric in the north than in the south, a result of less precipitation and more persistent winds that produce high evaporation rates (Visher 1954, U.S. Dept. of Commerce 1973-1983). These environmental gradients may explain the higher woody plant cover in the south than in the north (National Park Service 2001). A varied topography across the Loess Hills also produces a diversity of

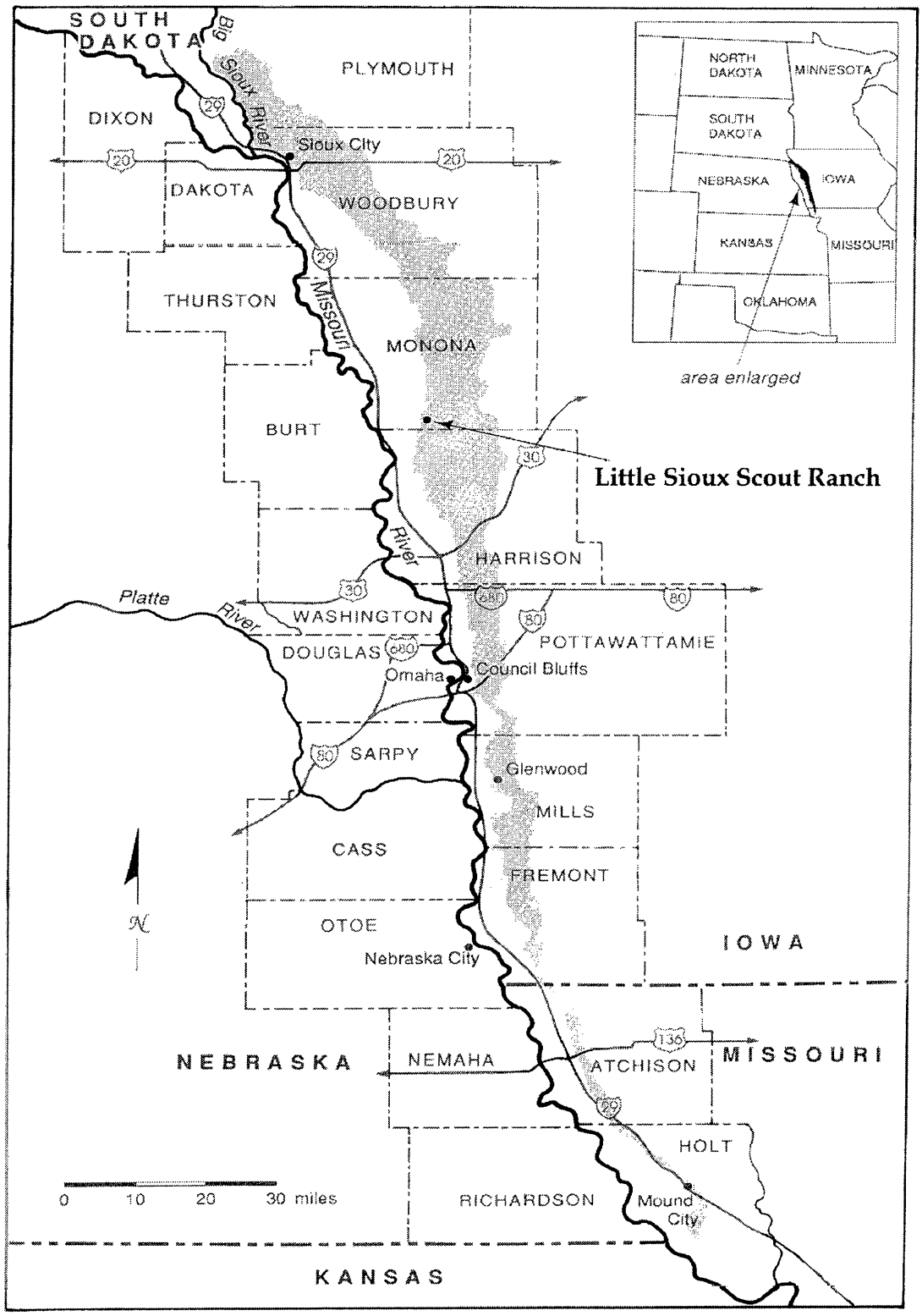


Fig. 1. The Iowa Loess Hills landform (shaded area) (Mutel 1989) and location of the Little Sioux Scout Ranch research site.

microclimates (Prior *et al.* 1984, Bettis *et al.* 1986). South- and west-facing slopes, for example, receive more sunlight and wind which may explain their support of most remnant prairie communities, while north- and east-facing slopes, typically shielded more from the sun and wind, support woodlands (Hanson 1922, Costello 1931, Rosburg and Glenn-Lewin 1996). This distribution of grassland and woodland communities, however, is not expected to persist (Costello 1931, Heineman 1982).

While the climate of the Loess Hills is capable of supporting woodland communities (Loomis and McComb 1944), trees in the region, historically, were largely absent. For example, in 1853, the General Land Office field survey notes for Monona County, Iowa, described the area as "all prairie no timber in it except for willows and scattering Cottonwood along the stream...entirely consists of rolling prairie." Today, however, the county, a microcosm of the larger landform, is largely tree-covered (Heineman 1982).

Despite the substantial loss of prairie in the region, the Loess Hills landform contains the majority of the entire state's extant native prairie, of which less than 0.05% (Smith 1998) of the original 12.5 million ha remains (Samson and Knopf 1994). Here, native prairie occurs in isolated remnants where slopes are too steep to plow (Schennum 1984, Smith 1998). Because of their fragmented distribution, further loss of prairie in the Loess Hills is of concern with invasion by woody plants considered to be one of the greatest threats (Heineman 1982, Schennum 1986). Already, forest cover of the Loess Hills has increased substantially since European settlement (Costello 1931, Loomis and McComb 1944, Kucera 1960, Heineman 1982) and present management is likely to

continue this trend, as it has throughout much of the eastern Great Plains (Costello 1931, Loomis and McComb 1944, Kucera 1960, Bragg and Hulbert 1976, Heineman 1982, McClain and Anderson 1990). In the Loess Hills, for example, Heineman (1982), predicted that woody species would completely replace prairie by 2060, at least that of Monona County, Iowa.

The composition of forests of the Loess Hills region has been variously described to be dominated by oak-hickory (*Quercus-Corya*) (Loomis and McComb 1944) or linden-ironwood (*Tilia americana-Ostrya virginiana*) (Costello 1931). These studies, however, were only qualitative observations of dominant species, presented without quantification and without reference to specific topographic location or temporal stability. Heineman (1982), in a quantitative study, described a bur oak-hackberry (*Quercus macrocarpa-Celtis occidentalis*) association on upper-slope locations, although he did not suggest that this would be a stable community. In another quantitative study, but one focused on one site at which no ridge-top prairie remained, Phillips (2001) suggested that various climax communities may exist depending on their topographic location, although all were dominated by a hackberry-ironwood association. Differences among these studies may be a function of many factors including community age, randomness of seed dispersal, or latitudinal location. For example, bitternut hickory (*Carya cordiformis*) decreases in abundance from southern to more northern latitudes and thus may not be a dominant species in more northern woodlands. Hackberry, however, occurs throughout and may replace hickory in more northerly locations (Stephens 1973, Novacek *et al.* 1985).

Given that woody plant encroachment is a relatively recent phenomenon, Loess Hills woodlands today are most likely to be seral communities of different ages varying by aspect and topographic position. Costello (1931) and Heineman (1982) suggested that woody plant expansion occurred as an upslope migration whereby lower slope forests should represent more mature forests than those further upslope. Costello (1931) also noted that succession should proceed more rapidly on more mesic north- and east-facing slopes than on more xeric south- and west-facing slopes. This observation is consistent with the present forest-domination of many north-facing slopes whereas prairies are mostly limited to upper south-facing slopes or along ridge-tops. This difference in rate of woody encroachment is also apparent in those areas where forests do not extend to ridge-tops. In these instances, the forest-prairie ecotone is typically further upslope on north than on south aspects (personal observation). From these observations, one can infer that woody communities of north aspects should be more mature, representing later successional stages, than woody communities of south aspects at the same elevation. Previous studies designed to test these specific hypotheses, however, are generally lacking. Moreover, the only detailed, quantitative study designed to assess the lowland-ridge-top coenocline did not support an upslope migration. Phillips (2001), in a dendrochronological evaluation, suggested an "individualistic colonization" of the Loess Hills. He hypothesized that extant woodlands resulted from expansion from randomly established individual trees patchily spaced, savanna-like, across the entire topographic gradient.

While previous studies and observations assessed different aspects of woody species encroachment, with the exception of Philips' (2001) dendrochronological study of a west-facing slope, none attempted to quantify the species composition of the lowland-ridge-top coenocline. Neither has there been an attempt to quantify overall woody plant encroachment at the expense of Loess Hills prairie. My study is designed to address both of these issues while also using results to hypothesize likely successional changes for the region.

Methods

This study had two components, (1) quantification of woody encroachment and (2) quantitative description of extant Loess Hills woodlands.

Quantification of Woody Encroachment.

To quantify woody encroachment at a regional scale between 1855 and 2000, my study focused on a three-county region. Monona County was chosen because it was the location both of my field site and of a site evaluated in 1981 (Heineman 1982). The counties to the north (Woodbury) and south (Harrison) were included to expand to a more regional scale (Fig. 1). These three counties also contain the majority of the remaining Loess Hills prairie (National Park Service 2001).

The external boundary of the Loess Hills landform, while indistinct on the ground on the eastern side, has been identified by the Iowa Geological Survey Bureau using specific parameters such as drainage density, drainage divides, density of isolated

hillforms, crenulated contours, slopes >15%, presence of catstep features, general loess thickness, and earlier mapping (Prior and Kourt 2002). Within this boundary, and as a consequence of the nation-wide General Land Office survey conducted in the 1800s, the Loess Hills landform is subdivided into a grid of *townships* with thirty-six 1.6 by 1.6 km (1 by 1 mile) *sections* making up each township. For this study, the section was established as the base unit for assessing woody plant encroachment, of which I included only those sections with >75% of their area occurring within the established boundaries of the Loess Hills. Of this subset of sections, I excluded those with more than 25% of their area occurring in major floodplains, defined as floodplains more than 1 km in width. Based on an analysis of topographic maps for the region, the 350-m elevation was determined to designate the upper elevation of these major floodplains. Floodplains were removed primarily because most of the low-lying valleys are farmed so woody plant invasion is not possible (personal observation). Finally, I also excluded sections that were >75% within major metropolitan areas, all of which were found to occur in the vicinity of Sioux City, Iowa.

Two sources of data were used to quantify woody encroachment: (1) General Land Office (GLO) field survey records and (2) aerial photographs. The GLO field surveys for the counties used in this study were completed between 1851and 1855 and digitized as vector-based GIS vegetation maps in 1996 (Anderson 1996). While there are limitations to the use of GLO survey data, including lack of surveyor knowledge of vegetation and accuracy of describing vegetative boundaries (Miller 1995), these potential inaccuracies were considered to be relatively minor given the resolution of this

aspect of the study. Importantly, these records provide the only quantitative information available for categorizing vegetative cover in the 1850s, and they do so by section number. Aerial photographs, against which the GLO survey notes were compared, were high-altitude, color infra-red photographs taken in July of 2000 and obtained from the Iowa Geological Survey Bureau. Sections were identified on aerial photographs using distinct property lines and roads that follow section boundaries.

For both the digitized General Land Office field survey maps (Anderson 1996) and the 2000 aerial photographs, woody plant cover was evaluated visually using different sizes of acetate grid overlays to accommodate the different scales of GLO maps and aerial photographs. Overlays were divided into section-sized grids that were subdivided into nine grid squares to more finely tune the evaluation of cover. Each grid square (nine per section) was then categorized as either "*woody*" or "*other*" based on the category covering the greatest proportion of the grid square. Woody cover on aerial photographs was identified visually based on texture, darkness, and boundary shape. On the GLO survey, woody cover was based on polygons described as *timber*, *thicket*, *scattering trees*, or *part prairie/part timber* (Anderson 1996). Using these categories provided a conservative estimate such that woody cover was likely over-estimated for the 1850s. The category "*other*" refers to residential, prairie, agricultural, and wetland areas, most of which were not separable from the aerial photographs. Cover data were converted to percent cover of woody plants. Areal cover calculations were based on 29 ha/grid square.

Quantification of Woodland Composition.

Study Site.— Quantification of the extant woody communities of the Loess Hills was conducted at the Little Sioux Scout Ranch in Monona County, Iowa (41°53' N, 95°59' W) (Fig. 1). This site was selected because of its accessibility, known recent land-use history, and because this was the site of a previous study by Heineman (1982). The area was entirely wooded except for isolated prairie remnants found on some west- and south-facing ridge-tops.

Soils at the study site varied topographically but all were silty loams formed from loess-based parent material (White *et al.* 1959). Hamburg and Ida silty loams were generally found on steep slopes. Monona silty loams occupied gently sloping uplands. Castana silty loams were found in areas between uplands and valleys, with valleys dominated by Napier silty loams. All soils at the study site had formed under native prairie vegetation with the exception of the Napier series, which formed on illuvium from slope soils (White *et al.* 1959). Slopes at the study site varied from 10% to 66%. The climate of the study site is characteristic of the midcontinental United States with warm, moist summers and cold, dry winters. Average temperatures range from -5°C in January to 23°C in July, with annual precipitation averaging 740 mm (White *et al.* 1959).

Little is known about the land use of the site in the late 1800s. Throughout most of the early 1900s the land was used privately for hunting with little active management. In the 1920s, the site was managed as a State Game Preserve. The bottomlands were farmed and black walnuts were logged in the 1930s and later decades, although neither of these activities affected the portion of the hills used in this study (Heineman 2002, pers.

comm.). In 1969 the site was donated to the Mid-America Council of the Boy Scouts of America. Since then, active management has consisted only of mowing some valleys and ridge-tops for trails (Heineman 1982).

Data Collection.— Initially, this study was designed to assess temporal changes in woody species by comparing 2001 data from the present study with that from Heineman's (1982) study. An assessment of field procedures, however, determined that only south-facing ridge-tops, defined in the 1982 study as "bluff tops", were evaluated at that time. Further, the same ridge-top plots used in the earlier study could not be precisely relocated.

The two hill masses finally selected as sites for this study were the only ones at the study area with similar topography, size, presence of ridge-top prairie remnants, and certainty that they were the same hillmasses used by Heineman in 1981. By incorporating the two identifiable ridge-tops used in the 1981 study in the present study, I was able to provide a general trend in plant community change that occurred during this 20 year period of time for this topolocation. Evaluating additional aspects and topographic locations situated downslope from the two ridge-tops, however, provided a quantitative base for both current and future comparisons.

Field sampling procedures were designed to evaluate woody plant composition along a topographic, lower slope-ridge-top coenocline with three objectives: (1) to quantify the composition of extant forest communities, (2) to infer a regional pattern of ecological forest succession, and (3) to provide a data base against which to compare future reevaluations.

Data collection at each site was based on stratified sampling of six topolocations: ridge-top, middle-slope, and lower-slope locations of both north- and south-facing

aspects. Ridge-top locations were situated along ridges of each hill mass with north-facing ridge-tops (NRT) and south-facing ridge-tops (SRT) situated just off the crest of the hill mass but in their respective directions. Lower-slope topographic locations were situated near the base of each hill mass (NLS = north lower slopes and SLS = south lower slopes) with middle-slope locations situated approximately halfway between (NMS = north middle slopes and SMS = south middle slopes). Valleys adjacent to the hill masses were not evaluated because of numerous past and present disturbances, including tree removal.

At each topolocation, vegetation was evaluated along a transect that extended horizontally at approximately the same elevation. The length of the transect necessarily varied depending on availability of suitable terrain but generally ranged from 75 to 125 m. Along each transect, five 10 m by 10 m plots were systematically located with an estimated 5-15 m between plots. Within each plot, I recorded canopy cover for all woody species and for six additional categories: *total cover* and overall cover of *woody species*, *forbs*, *grasses*, *litter*, and *bare soil*. Canopy cover categories used were: 0%; <5%; 5-25%; 25-50%; 50-75%; 75-95%; 95-99%; and >99% (modified from Daubenmire 1959). Data were analyzed using mid-point values of each cover category. Nomenclature for species was taken from Stephens (1973) and Great Plains Flora Association (1986). Coordinates of most plots were recorded using a hand-held GPS to facilitate relocation for future study (Appendix Table 1).

Data Analysis.-- Between-site differences in canopy cover of each species at each topographic location were tested using a 2-factor *t*-Test to determine if sites could

be combined (Appendix Table 2). Of 150 comparisons, only 22 differed significantly between sites, and, of these, the difference in cover was <5% for nine species, mostly resulting from the presence or absence of a species. In addition, ordination of community data, more fully described below, generally suggested similar species composition at each site for all but south-facing middle-slopes. Together, these results were considered to be sufficient justification to combine replicates from each site to test for differences in canopy cover among topographic locations using ANOVA and Student-Neuman-Kuels (SNK) Multiple Comparison tests (Table 1). Individual plot data for 1981 could not be located, thereby precluding any statistical analyses between years.

Community level attributes were evaluated using Principal Components Analysis (PCA) (McCune and Mefford 1995). Correlation matrices were selected to weight species evenly. Detrended Correspondence Analysis (DCA) was not chosen because PCA's Euclidean features are preferred in studies such as this with short gradient lengths in which species response is assumed to be linear (ter Braak and Prentice 1998). Principle Component Analysis was also used to search for a gradient among topolocations from which to infer a potential sequence of seral communities such as one consistent with assumptions of a lowland to upland invasion. Species Richness (S) and the Shannon-Wiener Index (H') were calculated to measure within-habitat diversity (Magurran 1988). Percent Similarity (PS) was calculated to assess similarities between all topolocations and sites (Magurran 1988). Significant differences in diversity between topographic locations were calculated using the Shannon-Wiener Index (H') values and procedures described in Zar (1999).

Table 1. Species diversity and mean percent canopy cover ± Standard Error for combined ridges with Student-Newman-Kuels groupings and associated *p*-values. Values with different superscripts among topolocations differ significantly. Communities are arranged along a hypothesized successional gradient from early stages (SRT) to late stages (NLS). SRT = South Ridge-Top, NRT = North Ridge- Top, SMS = South Middle Slope, NMS = North Middle Slope, SLS = South Lower Slope, NLS = North Lower Slope; tr ≤ 0.05% cover. na = not applicable; high H' value = high within-habitat diversity.

	TOPOGRAPHIC LOCATION						
	SRT	NRT	SMS	NMS	SLS	NLS	*p* value
Species Diversity							
Shannon-Wiener (H')	0.7363	0.6388	0.7156	0.6623	0.7908	0.7408	na
Species Richness	7	12	18	12	15	16	na
General Categories							
Total Cover	91^{b}±2.0	100^{a}±0	100^{a}±0	100^{a}±0	100^{a}±0	100^{a}±0	<.0001
Litter	72^{b}±6.7	75^{b}±5.6	91^{a}±3.7	98^{a}±0.4	98^{a}±0.4	97^{a}±1.4	<.0001
Soil	5^{a}±1.8	10^{a}±2.0	3^{ab}±1.4	1^{c}±0.3	1^{abc}±0.3	tr^{bc}	0.0001
Grass	80^{a}±3.0	4^{b}±1.8	1^{b}±0.3	1^{b}±0.3	2^{b}±0.3	8^{b}±6.1	<.0001
Forb	11^{b}±1.9	3^{c}±1.4	3^{c}±1.4	18^{b}±7.6	16^{b}±6.3	57^{a}±7 7	<.0001
Woody	20^{b}±3.0	100^{a}±0	100^{a}±0	100^{a}±0	100^{a}±0	100^{a}±0	<.0001
Prairie Woody Species							
New Jersey tea (*Ceanothus herbaceus*)	tr^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0.0624
Forest Woody Species							
Eastern red cedar (*Juniperus virginiana*)	10^{a}±3.7	10^{a}±3.7	7^{b}±3.9	0^{c}	0^{c}	0^{c}	<.0001
Smooth sumac (*Rhus glabra*)	12^{a}±3.6	5^{a}±1.7	4^{b}±3.7	0^{b}	0^{b}	0^{b}	<.0001
Rough-leaved dogwood (*Cornus drummondii*)	5^{bcd}±2.2	2^{bc}±1.4	45^{ab}±15.2	4^{cd}±3.7	42^{a}±12.9	0^{d}	<.0001

Table 1. Mean percent canopy cover ± Standard Error for combined ridges with SNK groupings and associated *p*-values. (Cont.)

	TOPOGRAPHIC LOCATION						
	SRT	NRT	SMS	NMS	SLS	NLS	*p* value
Green ash (*Fraxinus pennsylvanica*)	2^{b}±1.5	9^{a}±3.8	2^{ab}±1.5	tr^{ab}	tr^{b}	1^{ab}±0.4	0.014
Ironwood (*Ostrya virginiana*)	8^{b}±2.3	86^{a}±4.3	62^{a}±11.8	83^{a}±6.9	40^{ab}±10.7	69^{a}±11.0	0.0027
Bur oak (*Quercus macrocarpa*)	8^{b}±3.6	55^{ab}±15.0	66^{ab}±13.2	54^{ab}±8.8	98^{a}±1.4	8^{c}±6.2	<.0001
Riverbank grape (*Vitis riparia*)	0^{a}	tr^{a}	tr^{a}	tr^{a}	tr^{a}	0^{a}	0.5259
Bristly greenbrier (*Smilax hispida*)	0^{b}	2^{b}±1.5	tr^{ab}	2^{a}±1.4	1^{a}±0.4	tr^{b}	0.0002
Wild gooseberry (*Ribes missouriense*)	0^{c}	5^{ab}±2.2	1^{bc}±0.3	4^{ab}±1.9	15^{a}±4.2	6^{ab}±2.1	0.0007
Virginia Creeper (*Parthenocissus* spp)[a]	0^{c}	6^{a}±2.1	1^{b}±0.4	9^{a}±3.8	20^{a}±5.4	19^{a}±6.5	<.0001
Hackberry (*Celtis occidentalis*)	0^{d}	tr^{cd}	5^{bc}±2.2	15^{ab}±4.2	24^{a}±7.0	7^{cb}±3.9	<.0001
Choke cherry (*Prunus virginiana*)	0^{a}	tr^{a}	0^{a}	0^{a}	tr^{a}	1^{a}±0.4	0.0873
Bittersweet (*Celastrus scandens*)	0^{a}	0^{a}	tr^{ab}	0^{a}	0^{a}	0^{a}	0.4267
Black walnut (*Juglans nigra*)	0^{a}	0^{a}	2^{ab}±1.5	0^{a}	0^{a}	0^{a}	0.4267
Red mulberry (*Morus rubra*)	0^{a}	0^{a}	4^{a}±3.8	0^{a}	0^{a}	0^{a}	0.4267
American linden (*Tilia americana*)	0^{b}	0^{b}	tr^{b}	0^{b}	tr^{b}	40^{a}±16.1	0.0021
Wolfberry (*Symphoricarpos* spp)[b]	0^{c}	0^{c}	2^{b}±1.5	1^{bc}±0.3	15^{a}±3	2^{bc}±1.5	<.0001
Poison ivy (*Toxicodendron radicans*)	0^{c}	0^{c}	tr^{bc}	9^{ab}±8.5	6^{abc}±6.2	1^{a}±0.4	0.0026
Bitternut hickory (*Carya cordiformis*)	0^{b}	0^{b}	tr^{ab}	2^{a}±1.5	0^{b}	tr^{a}	0.0023
Moonseed (*Menispermum canadense*)	0^{a}	0^{a}	0^{a}	0^{a}	tr^{a}	0^{a}	0.4267
Prickly ash (*Zanthoxylum americanum*)	0^{a}	0^{a}	0^{a}	0^{a}	tr^{a}	1^{a}±0.4	0.0366
Elm (*Ulmus* spp)[c]	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	2^{a}±1.5	0.0645
Kentucky coffee tree (*Gymnocladus dioica*)	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	2^{a}±1.5	0.0727
Bladdernut (*Staphylea trifolia*)	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	tr^{a}	0.4267

Table 1. Mean percent canopy cover ± Standard Error for combined ridges with SNK groupings and associated *p*-values. (Cont.)

[a] While most likely *Parthenocissus quinquefolia*, *Parthenocissus vitacea* may also be represented.

[b] While most likely *Symphoricarpos occidentalis*, *Symphoricarpos orbiculatus* may also be represented.

[c] Includes both *Ulmus Americana* and *Ulmus rubra*.

Inferring Community Succession.

In the absence of a more reasonable alternative, data from the present study were used to speculate on what might constitute woody community succession over time in the Loess Hills. Inferring temporal changes in plant communities from the spatial distribution of species is presumptuous in relatively homogenous terrain but is even more so where terrain features, such as slope and aspect, impose a diversity of environmental conditions that may affect community dynamics. Significant environmental changes, such as those accompanying global warming, may yet further complicate any assessment. Nevertheless, there is value in attempting to provide an interim description of community succession, particularly one that can later be tested by reassessing the sites on which the speculation was based. However, additional studies elsewhere in the region would be required to characterize community changes in the Loess Hills as a whole.

Phillips (2001) suggested an "individualistic succession" of plant communities not initiated from lowlands, but instead resulting from "patch-expansion", that is by expansion of woody plants into the adjacent prairie matrix initiating from established individual trees randomly spaced across the topographic gradient. The premise on which the present study predicted temporal changes, however, was based on the more commonly reported assumption that woody plant establishment is initiated in the lowlands and expands upslope through slopes to ridge-tops, with the more mesic north-facing aspects invaded before their more xeric south-facing counterparts (Costello 1931, Heineman 1982). Such an expansion, however, does not preclude a subordinate process of patch expansion (Phillips 2001). Given the logic of upslope expansion, and the

assumption that many dominant woody species of the region have the potential to occupy a wide range of topographic locations in time, the earliest seral communities should occur on south-facing ridge-tops while the most mature communities should occur on north-facing lower slopes. While this is more of a Clementsian than a Gleasonian assumption, there is some support for this hypothesis. For example, American linden, currently a dominant lower slope species, is often found as seedlings and saplings on upper slopes and ridge-tops throughout the central and northern Loess Hills (Bragg 2002, pers. comm.). While this does not necessarily mean these individuals will survive, it does suggest their potential to mature where environmental conditions are consistent with each species' niche requirements. Further, given the relatively low diversity of woody plants at the latitude of the study site (Glenn-Lewin 1977), it would not be surprising to find differences in the composition of more mature forests in different topolocations ultimately to be reflected in the proportion of each species found rather than in a different array of species. While these various assumptions are substantial, they provide a theoretical base to justify an initial assessment of woody plant succession in the Loess Hills, at least until either more comprehensive ecosystem-wide studies are developed or until longer-term studies are available.

Results and Discussion

Change in Woody Cover.

In the 1850s, woody plants covered an average of 7% of the Loess Hills in the three-county area evaluated, although the amount varied from Woodbury County in the

north (3%; 1,842 ha) to Monona County (7%; 2,735 ha) to Harrison County in the south (16%; 4,491 ha) (Fig. 2). This result was similar to that reported by Davidson (1961), although his data included the counties as a whole, not just the Loess Hills portion of each: 4% (8,043 ha) in Woodbury County, 11% (19,898 ha) in Monona County, and 14% (26,074 ha) in Harrison County.

Between the 1850s and 2000, woody plant cover increased an average of 18% with the greatest increase (+38%) occurring in Monona County (Fig. 2). The overall increase is lower than the 66% increase for the county calculated by Heineman (1982) for the period 1853 and 1981, although his projection was based on data only from ridge-tops at a single site. Woody cover increases in this study were not clearly related to their latitudinal location where greater increases were expected to occur in the southern Loess Hills. This result suggests that some factor other than climate may affect woody plant encroachment. Personal observations suggest that slope steepness may be one factor explaining these different rates of encroachment. Specifically, the Loess Hills in Monona County contain the steepest topography within the landform, a characteristic making the landscape of that county less likely to be affected by anthropogenic factors, such as row agriculture and development, preempting land that may otherwise have been subject to woody plant invasion. Latitudinal location, however, may play some role as well. For example, the relatively low increase in woody cover (+7%) noted for Woodbury County, the most northern of the counties evaluated, may be due to environmental conditions being less favorable to woody plant growth, as previously discussed. In addition, row agriculture was more common in Woodbury

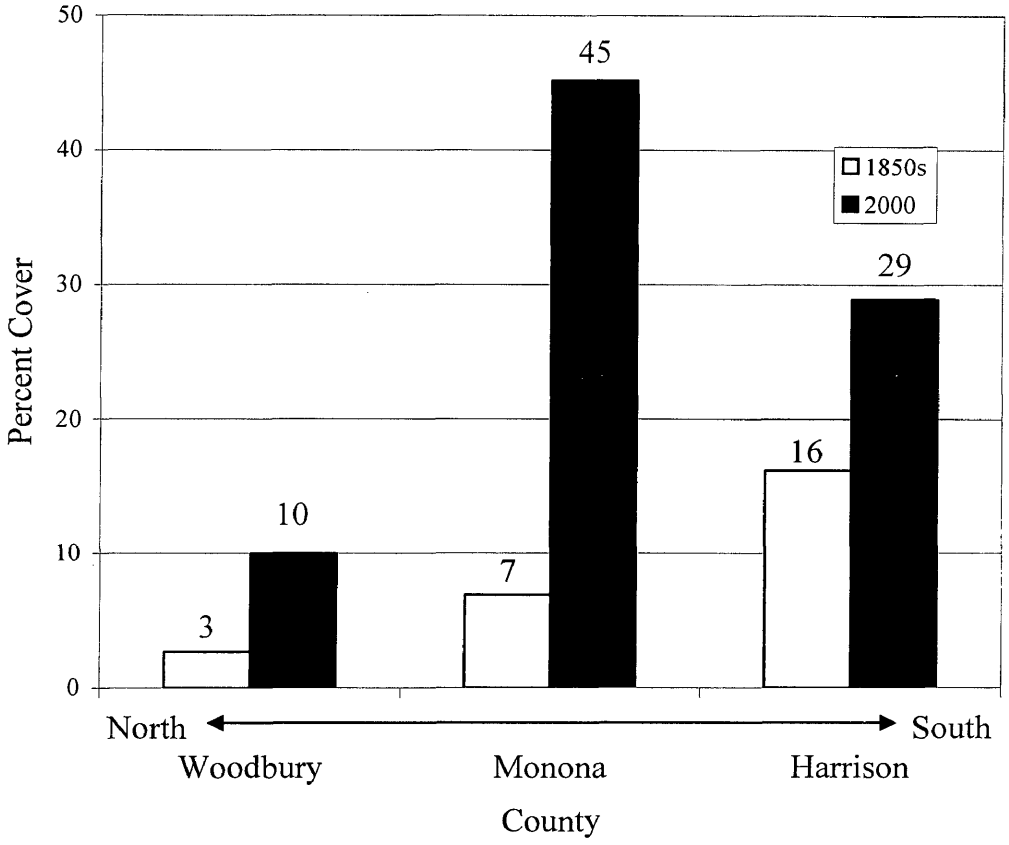


Fig. 2. Loess Hills woody plant cover in the 1850s and 2000 by county, excluding floodplains and areas presently within major cities.

County than in the other two counties (personal observation), which may also explain the relatively low woody cover.

Change in Ridge-Top Species Composition: 1981-2001.

Between 1981 and 2001 three general trends in species composition were observed along ridge-tops. The first was a general decline in prairie woody species, such as leadplant (*Amorpha canescens*) (Fig. 3, Table 2). While not unexpected, this response can only be inferred from this study since different prairie woody species were observed in the 1981 and 2001 studies, most likely because I was unable to relocate precisely the 1981 plots. The second temporal trend in woody plant cover was a decline in early seral woody species such as rough-leaved dogwood (*Cornus drummondii*) (-12%). A decline in such species was consistent with that expected to occur during ecological succession (Bragg 1974, McClain and Anderson 1990). A third trend was an increase in species known to occur in mid-sere communities (e.g. eastern red cedar; +7%), ironwood (+2%), green ash (+2%), and bur oak (+1%). In the absence of the original 1981 data set, however, the statistical significance of these changes could not be determined.

Composition of Topographic Coenocline.

While most likely transitory, four sometimes only subtly different plant communities appear to dominate the present Loess Hills woodland canopy at the study site: (1) smooth sumac-eastern red cedar (*Rhus glabra-Juniperus virginiana*) on south-facing ridge-tops, (2) bur oak-ironwood (*Quercus macrocarpa-Ostrya virginiana*) on

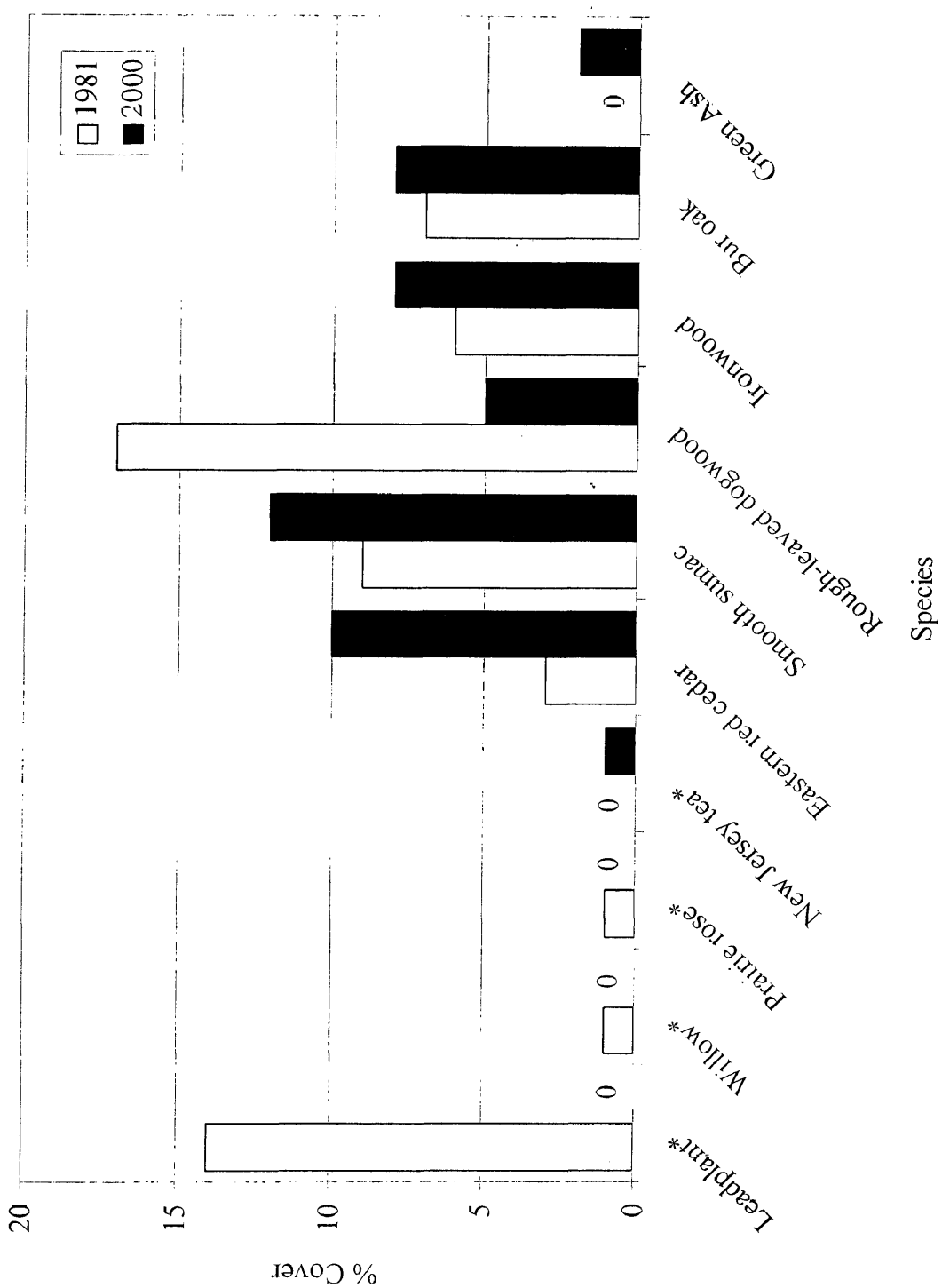


Fig. 3. Canopy cover of woody species on south-facing hilltops recorded by either Heineman (1982) or this study (2000) (Table 2). * = Woody species common in Loess Hills prairies.

Table 2. Canopy cover of woody species on south-facing hilltops in 1981 (Heineman 1982) and 2000. * = native woody species of Loess Hills prairies; tr = ≤ 0.05%

Species	Cover	
	1981	2000
Leadplant*	14	0
New Jersey tea*	0	tr
Sumac	9	12
Eastern red cedar	3	10

north-facing ridge-tops and north- and south-facing middle slopes, (3) bur oak-ironwood (*Quercus macrocarpa-Ostrya virginiana*) on south-facing lower slopes, distinguished from earlier successional stages by significantly greater amounts of understory species such as wild gooseberry (*Ribes missouriense*) and wolfberry (*Symphoricarpos* spp), and (4) ironwood-American linden (*Ostrya virginiana-Tilia americana*) on north-facing lower slopes (Table 1). The composition of north-facing lower slopes, however, differed significantly between sites with American linden (79% cover) and ironwood (43%) the principal overstory species at one site while the second site was dominated by ironwood (96% cover) with considerably less bur oak, hackberry, and elm (*Ulmus* spp.) (each 4% cover), and no American linden.

Based on Species Richness (S), diversity was lowest on the south-facing ridge-tops (S = 7), considered in this study to represent an early seral community of Loess Hills woodlands (Table 1). This result is consistent with general successional theory that suggests diversity increases with time (Odum 1969). In addition, Species Richness was highest (S = 18) on the south-facing middle slope topolocations, considered to represent a mid-successional stage, results consistent with the Intermediate Disturbance Hypothesis (Connell 1978), which predicts the highest diversity at some intermediate stage of succession.

While Species Richness values gave results consistent with general successional theory, results from Shannon-Wiener (H') diversity calculations, with the highest diversity at the south-facing lower slope (H' = 0.7908) and the lowest at the north-facing ridge-top (H' = 0.6388), were less so (Table 1). No logical biological explanation is

apparent for the different results from Species Richness and Shannon diversity calculations. Most likely, the differences represent artifacts of the types of analyses used. Shannon diversity, for example, measures the equitable distribution of species values (i.e. "cover" in this study) whereas Species Richness considers only the presence of a given number of species irrespective of their equitable distribution in cover.

Considering only Shannon diversity comparisons between all combinations of topolocations resulted in significant differences between north- and south-facing ridge-tops but not between north- and south-facing middle or lower slopes (Tables 1 and 3). Among other possibilities, this result suggests the obvious: Differences in diversity among wooded topolocations are fewer than differences in diversity between transitional prairie-woodland and wooded topolocations. In addition, the statistical comparison among topolocations shows south-facing lower slopes to differ most consistently from other topolocations with two comparisons differing significantly at $p \leq 0.05$ (the north-facing ridge-top and middle slope) and one (the south-facing middle slope) at $p \leq 0.10$. The biological logic of this result, however, is not apparent.

From Beta-diversity comparisons, which consider similarities in composition between sites, the topolocation that consistently differed the most from others was the south-facing ridge-top, the location that conceptually supported the most recently established community (Table 4). This result is not surprising since this was the only topolocation supporting prairie species. Topolocations that were the most similar based on Beta-diversity calculations were the north-facing middle slope and ridge-top and the south-facing middle slope and north-facing ridge-top followed by the south-facing middle

Table 3. Comparison of Shannon-Wiener (H') diversity between topographic locations based on procedures described in Zar (1999). Numbers shown in the matrix are *p*-values. An asterisk (*) indicates a significant difference in diversity between the two topographic locations at $\alpha = 0.05$. Communities are arranged along a hypothesized successional gradient from early stages (SRT) to late stages (NLS). SRT = South Ridge-Top, NRT = North Ridge-Top, SMS = South Middle Slope, NMS = North Middle Slope, SLS = South Lower Slope, NLS = North Lower Slope.

		Topographic Location					
		SRT	NRT	SMS	NMS	SLS	NLS
Topographic Location	SRT	—	*0.0352	0.6350	0.1009	0.1397	0.9276
	NRT		—	0.1086	0.6312	*0.0003	0.0546
	SMS			—	0.2547	0.0549	0.6205
	NMS				—	*0.0017	0.1318
	SLS					—	0.9815
	NLS						—

Table 4. Beta diversity (Percent Similarity) comparison matrix between topographic locations. High values indicate greater similarities between communities. Communities are arranged along a hypothesized successional gradient from early stages (SRT) to late stages (NLS). SRT = South Ridge-Top, NRT = North Ridge-Top, SMS = South Middle Slope, NMS = North Middle Slope, SLS = South Lower Slope, NLS = North Lower Slope. High value = high similarity.

		Topographic Location					
		SRT	NRT	SMS	NMS	SLS	NLS
Topographic Location	SRT	—	0.3084	0.2753	0.1786	0.1389	0.1650
	NRT		—	0.7076	0.8345	0.4983	0.5292
	SMS			—	0.6727	0.6816	0.4499
	NMS				—	0.6027	0.5835
	SLS					—	0.4028
	NLS						—

slope and lower slope and both north- and south-facing middle slopes. Taken together, these results indicate that middle slopes and south-facing lower slopes, all considered to be some stage of mid-sere community in this study, did not differ substantially, results consistent with community composition discussed earlier (Table 1).

Topographic Distribution of Individual Species.

As with communities, assessing the distribution of individual species across a topographic-aspect gradient provides some insight into that species' place in ecological succession of woody plants in Iowa's Loess Hills, keeping in mind the same qualifications previously discussed regarding the relationship between topographic location and seral status. Four patterns of species distribution were observed in this study: (1) a decline in a species' cover from ridge-tops to lower slopes, (2) a Gaussian distribution reflecting an increase in cover from ridge-tops to middle slopes with a decrease in cover from middle to lower slopes, (3) an increase in cover from ridge-tops to lower slopes, and (4) an even distribution of cover across topolocations.

The decline in cover from ridge-tops to lower slopes, observed for species such as New Jersey tea, eastern red cedar, and smooth sumac, was consistent with a temporal distribution of species that decline during ecological succession (Fig. 4, Table 1). The decline in these species most likely reflects their response to environmental conditions that shift either from more xeric conditions to less suitable mesic conditions or to lower light intensity, either shift resulting from an increasingly greater amount of tree canopy as

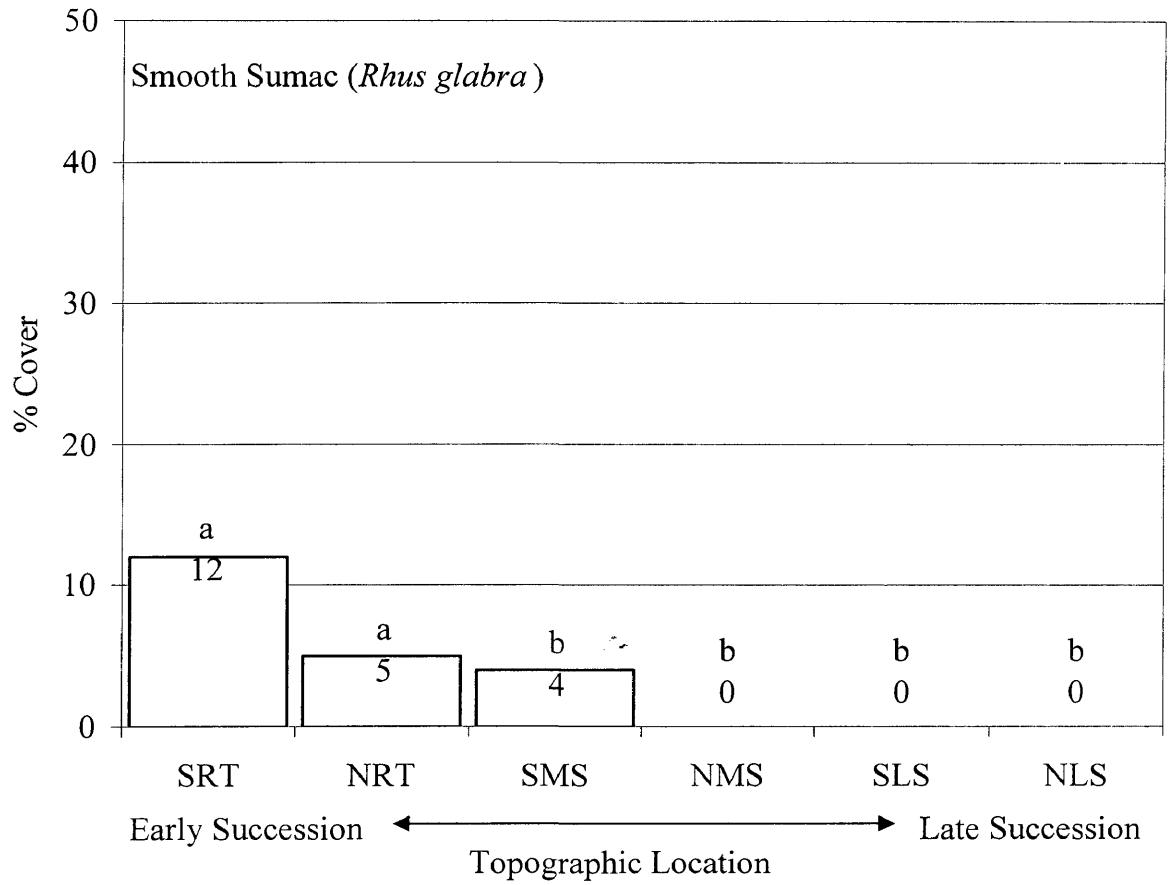


Fig. 4. Canopy cover of smooth sumac (*Rhus glabra*) across the hypothesized sere. SRT = South Ridge-Top, NRT = North Ridge-Top, SMS = South Middle Slope, NMS = North Middle Slope, SLS = South Lower Slope, and NLS = North Lower Slope. Bars with the same alphabetical superscript do not differ significantly ($\alpha = 0.05$; Student-Newman-Kuels). There were no significant differences in canopy cover of the species between the two hills at the topographic locations shown ($p \leq 0.05$; 2-factor *t*-Test).

woody plant encroachment moves upslope (Visher 1954, U.S. Dept. of Commerce 1973-1983).

The second pattern of species distribution was a bell-shaped, Gaussian pattern characteristic of mid-sere species encroaching into a new location (e.g. ridge-tops) while still dominating where they had been established for some time (e.g. middle slopes) yet being replaced by other species where they first were established (e.g. lower slopes). Species showing this pattern include bur oak and, to a lesser extent, rough-leaved dogwood (Fig. 5, Table 1). The decline in cover of these species from ridge-top to lower slope locations is consistent with their hypothesized decline with time, a conclusion supported by the absence of seedlings in all but open-canopy ridge-tops (personal observation). This distribution, however, neither supports nor refutes the hypothesis that bur oak occurred as scattered individuals throughout most topographic locations of the Loess Hills (Phillips 2001). Dogwood, another well-known invasive, woody species (Bragg 1974, McClain and Anderson 1990) most likely also invaded early but was able to persist for some time. Its uneven distribution reflects its proclivity to perpetuate expanding colonies where conditions are suitable to establishment.

The species distribution characterized by an increase in cover from ridge-tops to lower slopes is best shown for American linden, although Kentucky coffee tree (*Gymnocladus dioica*) and elm were recorded but only lower slopes (Fig. 6, Table 1). Both American linden and Kentucky coffee tree have been observed as both seedlings and saplings on upper slopes and occasionally on ridge-tops (Bragg 2003, pers. comm.) suggesting their ability to become established and perhaps develop into canopy trees

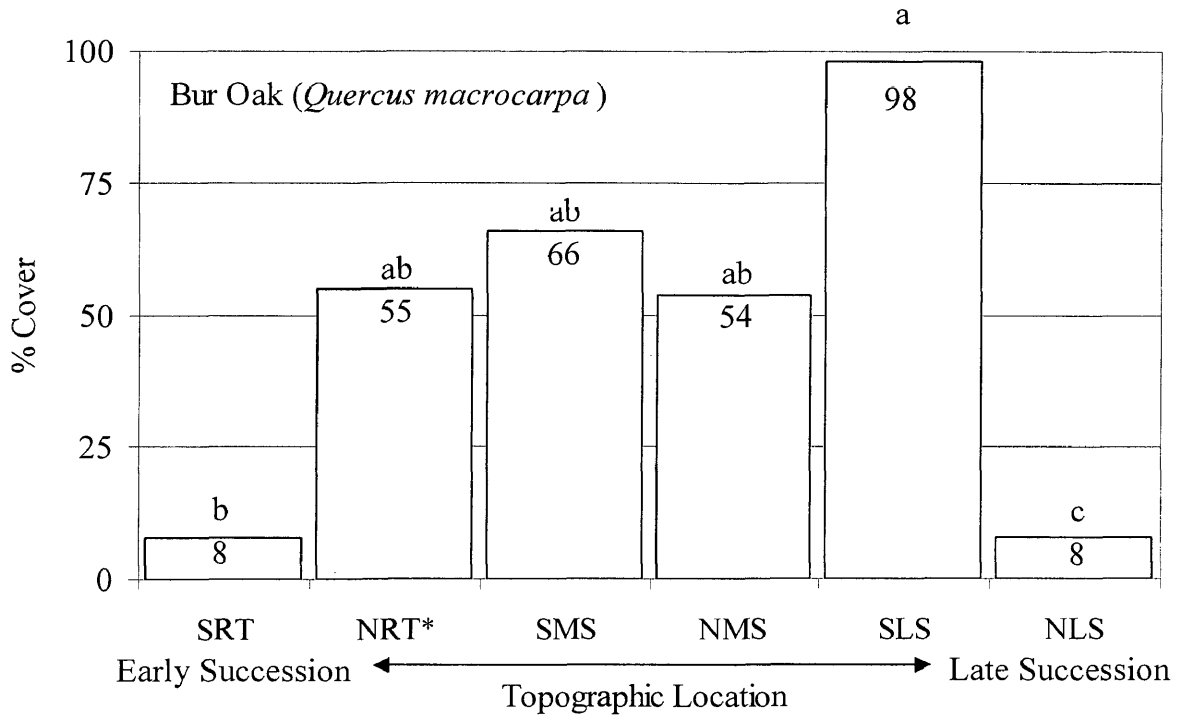


Fig. 5. Canopy cover of bur oak (*Quercus macrocarpa*) across the hypothesized sere. SRT = South Ridge-Top, NRT = North Ridge-Top, SMS = South Middle Slope, NMS = North Middle Slope, SLS = South Lower Slope, and NLS = North Lower Slope. Bars with the same alphabetical superscript do not differ significantly (α=0.05; Student-Newman-Kuels). An asterisk (*) indicates a significant difference in canopy cover between the two hills at the topographic location indicated ($p \leq 0.05$; 2-factor *t*-Test).

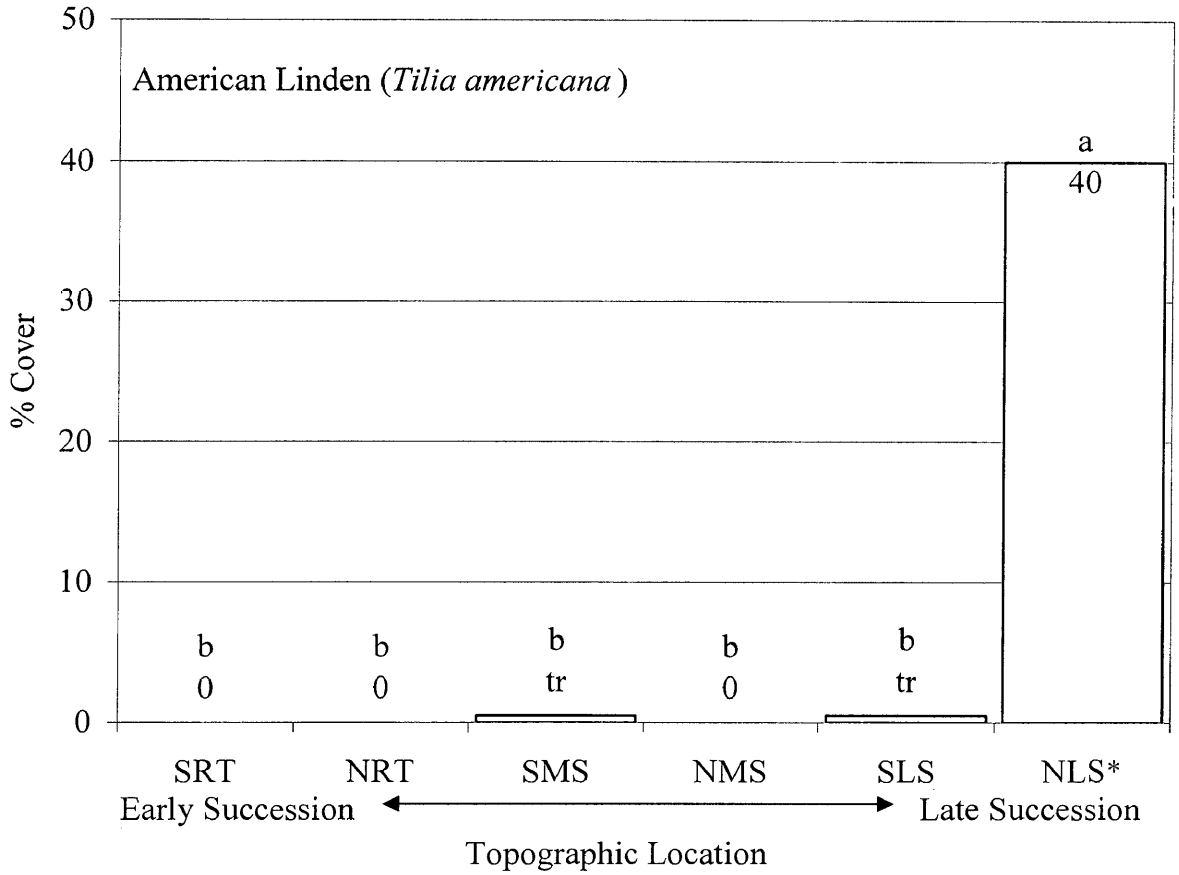


Fig. 6. Canopy cover of basswood (*Tilia Americana*) across the hypothesized sere. SRT = South Ridge-Top, NRT = North Ridge-Top, SMS = South Middle Slope, NMS = North Middle Slope, SLS = South Lower Slope, and NLS = North Lower Slope. Bars with the same alphabetical superscript do not differ significantly (α=0.05; Student-Newman-Kuels). An asterisk (*) indicates a significant difference in canopy cover between the two hills at the topographic location indicated ($p \leq 0.05$; 2-factor *t*-Test).

where environmental conditions are suitable. Virginia creeper (*Parthenocissus* spp) is a woody vine that shows a similar trend (Table 1). This type of spatial distribution is consistent with the temporal distribution of late successional species that require time for environmental conditions to be suitable for their successful establishment and development.

The final species distribution, characterized by high canopy cover in all but ridge-top communities represents woody species that rapidly colonize areas, particularly once some forest canopy cover is established, and then persist for long periods of time, often as understory or subcanopy species (Stephens 1973, Phillips 2001). Ironwood best represents this distribution (Fig. 7, Table 1). Ironwood is a shade tolerant woody species whose seeds are easily dispersed by animals and likely also by wind (Van Dersal 1939, Stephens 1973). While rarely found as a dominant canopy tree (personal observation), this species is a common subcanopy species that, in this study, was found to have an average canopy cover >40% in all but the south-facing ridge-tops hypothesized to be the earliest seral community.

Community Succession.

Principle Components Analysis of individual transects supported my hypothesis of a general successional gradient from ridge-tops to middle slopes to lower slopes (Fig. 8). In addition, except for lowlands where aspect is less likely to be a significant environmental factor, south aspects consistently occurred more towards what was hypothesized to be the earlier successional end of the gradient than did their north aspect

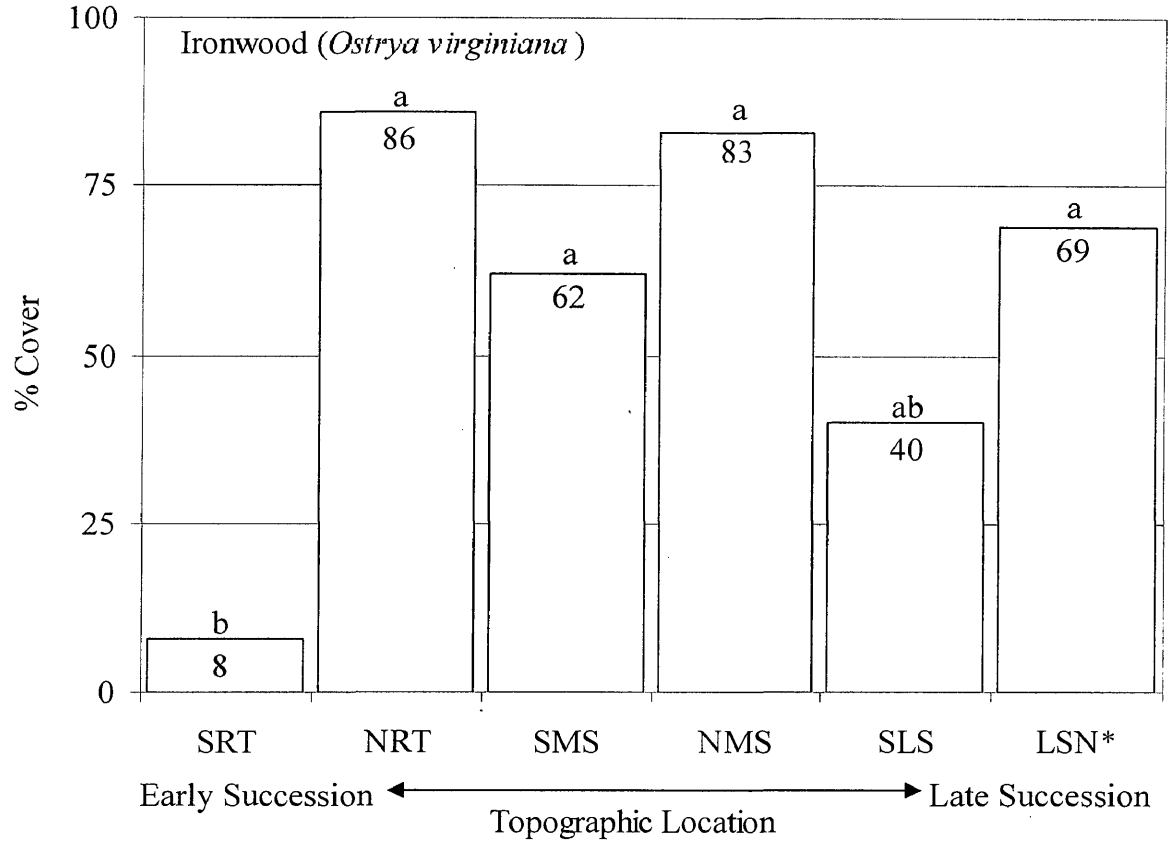


Fig. 7. Canopy cover of ironwood (*Ostrya virniniana*) across the hypothesized sere. SRT = South Ridge-Top, NRT = North Ridge-Top, SMS = South Middle Slope, NMS = North Middle Slope, SLS = South Lower Slope, and NLS = North Lower Slope. Bars with the same alphabetical superscript do not differ significantly (α=0.05; Student-Newman-Kuels). An asterisk (*) indicates a significant difference in canopy cover between the two hills at the topographic location indicated ($p \leq 0.05$; 2-factor *t*-Test).

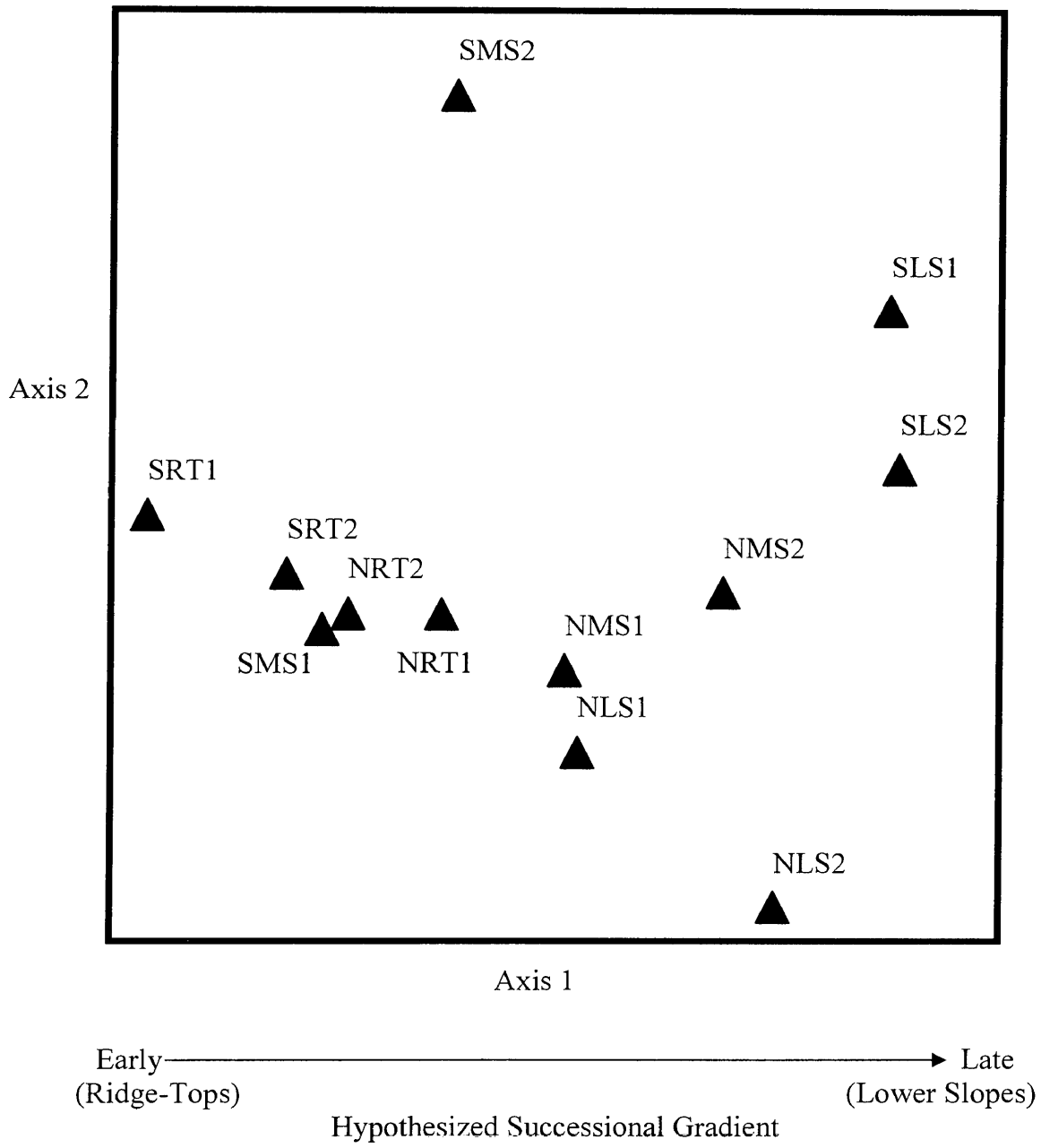


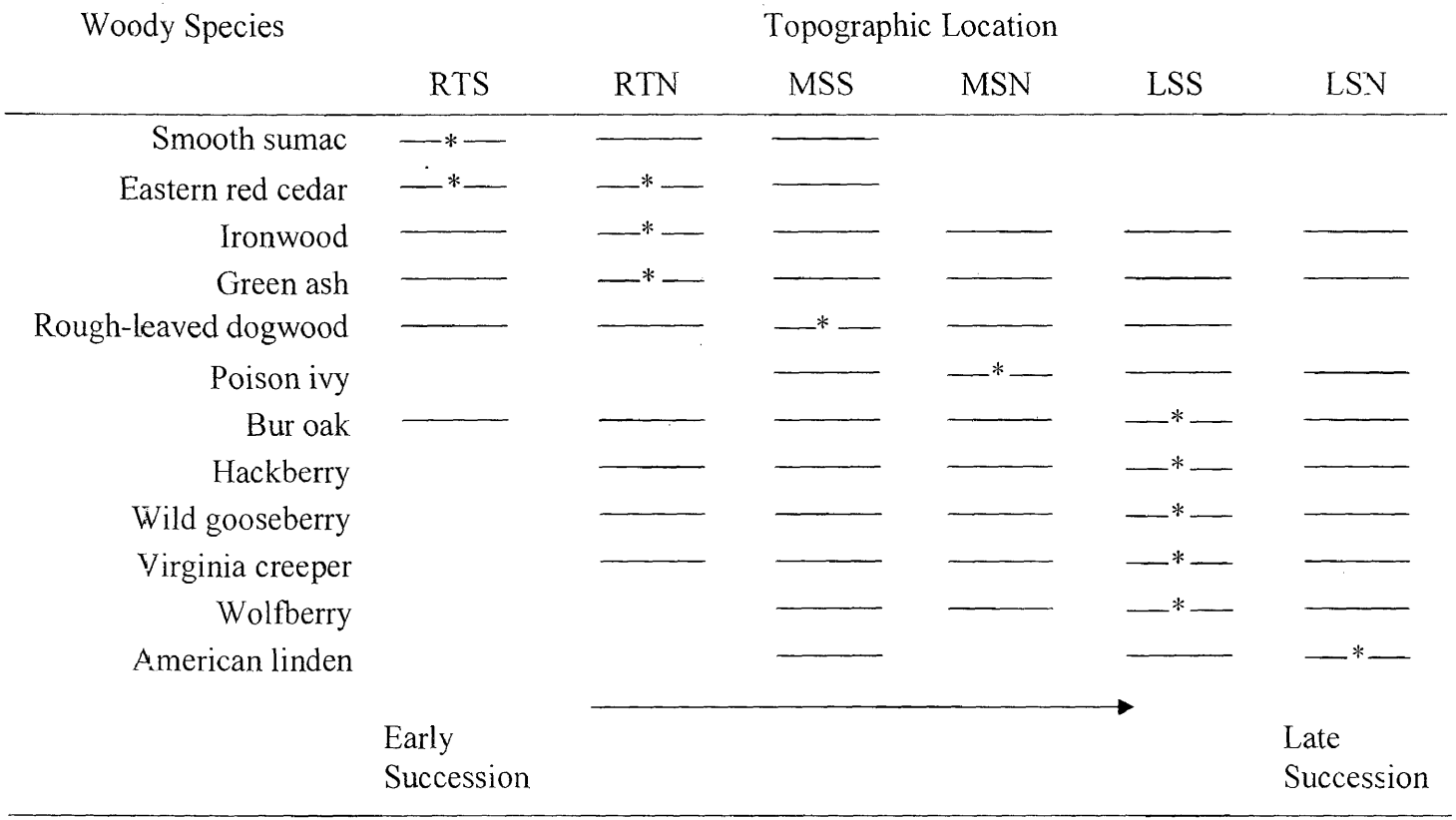
Fig. 8. Ordination of individual transects along the first two PCA axes. SLS = South Lower Slope, SMS = South Middle Slope, SRT = South Ridge-Top, NLS = North Lower Slope, NMS = North Middle Slope, and NRT = North Ridge-Top. Numbers following topolocations indicate site numbers. Eigenvalues: Axis 1 = 5.401 (23.5% of variance), Axis 2 = 4.166 (18.1% of variance). "Early" and "Late" refer to potential seral stages along a successional gradient.

counterpart, a result consistent with the hypothesized later woody plant invasion of southern than of northern aspects. However, since Axis 1 represents only 23.5% of the variance, factors other than topographic location are likely to be important in explaining the distribution of transects in ordination space. Identifiable patterns along other axes, however, were not apparent.

The distribution of communities in ordination space, adjusted to accommodate species composition for the lower slope where American linden is presumed to characterize the oldest forest stand, was the basis on which transects were arranged along a presumed successional gradient (Table 1). This gradient, consistent with those hypothesized by Costello (1931), Heineman (1982), and Phillips (2001), was the basis on which a proposed sere for the Loess Hills was developed.

Early Seral Communities. — Early seral communities, characterized by the vegetation of south-facing ridge-tops, supported remnant populations of prairie species, such as New Jersey tea (*Ceanothus herbaceus*) (<1%) but were dominated by early invaders including smooth sumac (12%), eastern red cedar (10%), bur oak (8%), and ironwood (8%) (Table 1, Fig. 9). Smooth sumac is a member of the shrub zone that is temporally and spatially located within the prairie-forest ecotone (Hanson 1922, Costello 1931) so its presence in an early seral woody community is not unexpected (Fig. 4). Eastern red cedar is also not unexpected as it has been noted as an early invader of the prairie (e.g. Bragg 1974) due to its ability to grow in xeric, upland soils and its dispersal by birds (e.g. Blewett 1984). The low canopy cover of ironwood (8%) largely reflects the beginning of invasion of this species into the prairie-forest margin where the

Fig. 9. Woody species with ≥ 10% canopy cover (Table 1) in at least one topographic location showing its occurrence within a proposed sere. SRT = South Ridge-Top, NRT = North Ridge-Top, SMS = South Middle Slope, NMS = North Middle Slope, SLS = South Lower Slope, and NLS = North Lower Slope. An asterisk (*) indicates the topographic location at which canopy cover of a species is highest.



microclimate is favorable for invaders (Behnke and Ebinger 1989). Finally, the low canopy cover of bur oak (8%) on south-facing slopes, reflects the presence of seedlings within the prairie matrix (personal observation), indicating the ability of this species to establish in the more xeric prairie interior. This may also explain its historic occurrence in scattered groves or as individuals distributed across all Loess Hills topographic locations, as hypothesized by Phillips (2001).

Mid-Sere Communities. — Except for north-facing lower slopes, hypothesized to be the most mature community, all other topolocations on slopes were dominated by a mix of bur oak and ironwood. These communities appear to represent various mid-sere compositions, although those with lower proportions of hackberry and understory shrubs, such as wild gooseberry and wolfberry, may be earlier in the successional process than those with higher proportions of these species (Fig. 9, Table 1). Ironwood, a common understory species in the Loess Hills (Stephens 1973), had high cover at all topolocations where woody cover was high. The bur oaks that dominate these mid-seral communities may be remnants of the historic bur oak savanna with the other woody species largely having subsequently invaded (Nuzzo 1986, Rosburg and Glenn-Lewin 1996) (Fig. 5). This pattern is a common occurrence in the absence of fire in savannas around the world (Moreira 2000). In addition, the high cover of bur oak across the slope is consistent with Phillip's (2001) conclusion that scattered bur oak occurred historically across all topographic locations. Previously established individuals maintain the dominance of this species in the canopy but poor bur oak regeneration (Phillips 2001, personal observation) in these communities signals some future end to its domination.

Late-Sere Communities. — The north-facing lower slope, hypothesized to be among the most mature woody communities of the region, was dominated by American linden (79%) and ironwood (43%) at one site, consistent with the "climax" community composition described by Costello (1931). The presence of Kentucky coffee tree in this setting, a species of low, rich woods (Great Plains Flora Association 1986), is further indication of the maturity of this site. At the other north-facing lower slope site, however, the forest canopy was dominated by ironwood (96%) with American linden and Kentucky coffee tree absent (Appendix Table 2). This difference suggests that the two sites, while both considered to be among the more mature forests, may represent substantial differences in environmental conditions among north-facing sites or it may indicate that the widespread distribution of a few large trees, such as the American linden found in the north-facing lower slope site, may not have been adequately sampled with the number of plots evaluated in this study. The presence of American linden and Kentucky coffee tree on north-facing lower slopes and their absence on south-facing lower slopes supports the proposition that communities of south-facing lower slopes are in an earlier state of succession than north-facing lower slopes. Variations in factors such as topography and climate, and associated environmental conditions, will determine how far upslope and on which aspects this mature community might develop.

Conclusion

Quantification of the extant forested community of the Iowa Loess Hills describes a topographic coenocline dominated on the ridge-tops by smooth sumac, eastern red cedar, and rough-leaved dogwood, on upper and middle slopes by bur oak and ironwood with some green ash or hackberry, and on lower slopes by American linden and ironwood. Given that this study also documents a loss of 18% of the original prairie since 1855 to woody plant encroachment, with losses continuing into the future, it is unlikely that these are self-perpetuating communities. Rather, inferences from the species composition of different topographic locations and aspects suggest a succession of species over time that approximates the community composition from upper to lower slopes – *New Jersey tea* to *eastern red cedar* to *bur oak-ironwood* to *American linden-ironwood* or *Kentucky coffee tree-ironwood* communities in the more mesic locations. Further, data support the hypothesis that woody expansion involves an upslope migration of species. These results, while requiring verification with further study, both expand our understanding of the biological processes occurring in the Loess Hills and provide important information relevant to making appropriate land management decisions in this important ecosystem.

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Appendix

Appendix Table 1. Coordinates of study plots at the Little Sioux Scout Ranch, Monona County, Iowa. Dashes indicate no data. Plots are ordered 1 through 5 at each topographic location, with number 1 being the easternmost plot. Topographic locations are ordered from the lower, north-facing slopes to the lower, south-facing slopes. SLS = South Lower Slope, SMS = South Middle Slope, SRT = South Ridge-Top, NRT = North Ridge-Top, NMS = North Middle Slope, NLS = North Lower Slope. NMS = North Middle Slope, SLS = South Lower Slope, NLS = North Lower Slope. For all measurements except the hilltops, coordinates were taken in the center of the plots. Since the NRT and SRT plots share a boundary at the peak of the hill, the hilltop coordinates taken represent the 5 m midpoint of the shared side.

Study Hillmass No. 1

Topolocation	Plot Number				
	1	2	3	4	5
SLS	——	——	——	——	41° 52.42' N 95° 57.31' W
SMS	——	——	——	41° 52.43' N 95° 57.23' W	——
SRT/NRT	41° 52.41' N 95° 57.21' W	41° 52.41' N 95° 57.26' W	41° 52.43' N 95° 57.26' W	41° 52.44' N 95° 57.29' W	41° 52.46' N 95° 57.34' W
NMS	——	——	41° 52.49' N 95° 57.32' W	41° 52.50' N 95° 57.31' W	41° 52.51' N 95° 57.31' W
NLS	——	——	——	41° 52.49' N 95° 57.31' W	——

Appendix Table 1. Coordinates of study plots at the Little Sioux Scout Ranch, Monona County, Iowa. (Continued)

Study Hillmass No. 2

Topolocation	Plot Number				
	1	2	3	4	5
SLS	——	——	——	——	41° 52.73' N 95° 57.28' W
SMS	41° 52.73' N 95° 57.27' W	41° 52.75' N 95° 57.27' W	——	41° 52.77' N 95° 57.29' W	41° 52.74' N 95° 57.29' W
SRT/NRT	41° 52.69' N 95° 57.23' W	41° 52.75' N 95° 57.26' W	41° 52.75' N 95° 57.29' W	41° 52.75' N 95° 57.30' W	41° 52.76' N 95° 57.31' W
NMS	——	41° 52.78' N 95° 57.26' W	41° 52.75' N 95° 57.28' W	——	41° 52.83' N 95° 57.31' W
NLS	41° 52.80' N 95° 57.28' W	41° 52.79' N 95° 57.28' W	——	41° 52.79' N 95° 57.29' W	——

Appendix Table 2. Mean percent canopy cover ± Standard Error with SNK groupings and associated *p*-values. Values with different superscripts among topographic locations differ significantly among topographic locations. Boxed values indicate significant differences in canopy cover for a category between the two hill masses (α=0.05), according to ANOVA. SRT = South Ridge-Top, NRT = North Ridge-Top, SMS = South Middle Slope, NMS = North Middle Slope, SLS = South Lower Slope, NLS = North Lower Slope; tr ≤ 0.05% cover.

		TOPOGRAPHIC LOCATION						
Floristics	Hill	SRT	NRT	SMS	NMS	SLS	NLS	*p* value
General Categories								
Total Cover	1	90^{b}±2.9	100^{a}±0	100^{a}±0	100^{a}±0	100^{a}±0	100^{a}±0	<.0001
	2	92^{b}±2.9	100^{a}±0	100^{a}±0	100^{a}±0	100^{a}±0	100^{a}±0	<.0001
Litter	1	57^{b}±9.0	62^{b}±7.5	83^{ab}±5.6	98^{a}±0.5	98^{a}±0.5	95^{a}±2.6	<.0001
	2	87^{b}±2.4	87^{b}±2.4	98^{a}±0.6	98^{a}±0.6	98^{a}±0.6	99^{a}±0.5	0.0007
Soil	1	5^{ab}±2.6	8^{a}±3.1	5^{ab}±2.6	tr^{c}	1^{ab}±0.4	tr^{bc}	0.0003
	2	5^{b}±2.6	12^{a}±2.5	1^{b}±0.5	1^{b}±0.5	1^{b}±0.5	1^{b}±0.4	0.0008
Grass	1	80^{a}±4.5	4^{b}±3.2	2^{b}±0.5	1^{b}±0.5	2^{b}±0.4	13^{b}±12.3	0.0023
	2	80^{a}±4.5	1^{c}±0.4	1^{c}±0.4	1^{bc}±0.5	1^{bc}±0.5	2^{b}±0	<.0001
Forb	1	10^{b}±3.1	5^{b}±2.5	1^{c}±0.4	29^{b}±13.9	5^{b}±2.5	57^{a}±9	<.0001
	2	12^{b}±2.5	1^{c}±0.4	5^{b}±2.5	8^{b}±3.1	26^{ab}±10.6	57^{a}±13.7	<.0001
Woody	1	20^{b}±4.5	100^{a}±0	100^{a}±0	100^{a}±0	100^{a}±0	100^{a}±0	<.0001
	2	20^{b}±4.5	100^{a}±0	100^{a}±0	100^{a}±0	100^{a}±0	100^{a}±0	<.0001
Prairie Woody Species								
New Jersey tea	1	tr^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0.0471
(*Ceanothus herbaceus*)	2	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	--

Appendix Table 2. Mean percent canopy cover ± Standard Error with SNK groupings and associated *p*-values. (Continued)

Floristics	Hill	TOPOGRAPHIC LOCATION SRT	NRT	SMS	NMS	SLS	NLS	*p* value
Forest Woody Species								
Eastern red cedar	1	$14^{a}\pm6.4$	$11^{a}\pm7.2$	$6^{a}\pm3.6$	0^{b}	0^{b}	0^{b}	<.0001
(*Juniperus virginiana*)	2	$6^{a}\pm3.6$	$10^{a}\pm3.1$	$8^{b}\pm7.5$	0^{b}	0^{b}	0^{b}	<.0001
Smooth sumac	1	$12^{a}\pm7.0$	$8^{a}\pm3.1$	8^{b}+7.5	0^{b}	0^{b}	0^{b}	<.0001
(*Rhus glabra*)	2	$12^{a}\pm3.0$	$2^{a}\pm0.4$	0^{b}	0^{b}	0^{b}	0^{b}	<.0001
Rough-leaved dogwood	1	$10^{ab}\pm3.4$	$4^{bc}\pm2.9$	$3^{bc}\pm3$	0^{c}	$44^{a}\pm20.2$	0^{c}	0.0004
(*Cornus drummondii*)	2	0^{c}	$1^{b}\pm0.4$	$87^{a}\pm12.4$	$8^{b}\pm7.3$	$40^{a}\pm18.3$	0^{c}	<0.0001
Green ash	1	$3^{a}\pm3.0$	$14^{a}\pm6.9$	0^{a}	0^{a}	tr^{a}	0^{a}	0.0381
(*Fraxinus pennsylvanica*)	2	0b	$4^{a}\pm2.8$	$4^{a}\pm2.7$	tr^{ab}	0^{b}	$2^{ab}\pm0.6$	0.0051
Ironwood	1	$4^{b}\pm2.8$	$81^{a}\pm8.0$	$89^{a}\pm7.4$	$77^{a}\pm11.9$	$26^{ab}\pm10.9$	$43^{a}\pm13.7$	0.0044
(*Ostrya virginiana*)	2	$12^{a}\pm2.9$	$90^{a}\pm2.9$	$35^{a}\pm14.4$	$90^{a}\pm6.9$	$55^{a}\pm17.2$	$96^{a}\pm2.7$	0.0558
Bur oak	1	$12^{a}\pm6.8$	$99^{a}\pm0.5$	$32^{a}\pm15.4$	$48^{a}\pm9.6$	$100^{a}\pm0$	$12^{b}\pm12$	<.0001
(*Quercus macrocarpa*)	2	$5^{b}\pm2.5$	$11^{b}\pm7.1$	$99^{a}\pm0.5$	$60^{ab}\pm15.4$	$96^{a}\pm2.8$	$4^{c}\pm2.9$	<.0001
Riverbank grape	1	0^{a}	tr^{a}	$1^{a}\pm0.5$	0^{a}	tr^{a}	0^{a}	0.4084
(*Vitis riparia*)	2	0^{a}	tr^{a}	0^{a}	tr^{a}	0^{a}	0^{a}	0.1778
Bristly greenbrier	1	0^{b}	$4^{ab}\pm2.9$	tr^{ab}	$3^{a}\pm2.9$	$1^{a}\pm0.5$	0^{b}	0.0021
(*Smilax hispida*)	2	0^{a}	0^{a}	tr^{a}	$1^{a}\pm0.6$	$1^{a}\pm0.6$	$1^{a}\pm0.5$	0.1033
Wild gooseberry	1	0^{b}	10^{a}+3.1	$1^{b}\pm0.6$	$1^{b}\pm0.6$	$24^{a}\pm5.5$	$1^{b}\pm0.6$	0.0002
(*Ribes missouriense*)	2	0^{b}	0^{b}	tr^{b}	$6^{ab}\pm3.5$	$6^{ab}\pm3.5$	$10^{a}\pm3.1$	0.0005
Virginia Creeper	1	0^{c}	10a+3.1	$1.7^{b}\pm0.5$	$1^{b}\pm0.4$	$17^{a}\pm5.9$	$5^{ab}\pm2.6$	<.0001
(*Parthenocissus* spp)[a]	2	0^{c}	$1^{b}\pm0.5$	0^{c}	$17^{a}\pm5.7$	$24^{a}\pm9.5$	$34^{a}\pm8.8$	<.0001

Appendix Table 2. Mean percent canopy cover ± Standard Error with SNK groupings and associated *p*-values. (Continued)

		TOPOGRAPHIC LOCATION						
Floristics	Hill	SRT	NRT	SMS	NMS	SLS	NLS	*p* value
Hackberry	1	0^{b}	$2^{ab}\pm0.6$	$4^{ab}\pm2.9$	$10^{a}\pm3.4$	$29^{a}\pm9.4$	$11^{ab}\pm7.2$	0.0101
(*Celtis occidentalis*)	2	0^{b}	0^{b}	$6^{ab}\pm3.7$	$21^{a}\pm7.3$	$20^{a}\pm11.1$	$4^{ab}\pm2.9$	0.0008
Choke cherry	1	0^{a}	$1^{a}\pm0.5$	0^{a}	0^{a}	0^{a}	$1^{a}\pm0.6$	0.1778
(*Prunus virginiana*)	2	0^{a}	0^{a}	0^{a}	0^{a}	tr^{a}	$1^{a}\pm0.5$	0.5579
Bittersweet	1	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	--
(*Celastrus scandens*)	2	0^{a}	0^{a}	tr^{a}	0^{a}	0^{a}	0^{a}	0.4389
Black walnut	1	0^{a}	0^{a}	$3^{a}\pm3$	0^{a}	0^{a}	0^{a}	0.4389
(*Juglans nigra*)	2	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	--
Morus rubra	1	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	--
(*Morus rubra*)	2	0^{a}	0^{a}	$8^{a}\pm7.5$	0^{a}	0^{a}	0^{a}	0.4389
American linden	1	0^{b}	0^{b}	$1^{b}\pm0$	0^{b}	tr^{b}	$79^{a}\pm19.8$	<.0001
(*Tilia americana*)	2	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	--
Wolfberry	1	0^{c}	0^{c}	$1^{b}\pm0.5$	0^{c}	$10^{a}\pm3.1$	tr^{bc}	<.0001
(*Symphoricarpos* spp)[b]	2	0^{b}	0^{b}	$4^{b}\pm2.9$	$1^{b}\pm0.6$	$20^{a}\pm4.5$	$3^{b}\pm3$	0.0005
Poison ivy	1	0^{a}	0^{a}	tr^{a}	tr^{a}	0^{a}	tr^{a}	0.067
(*Toxicodendron radicans*)	2	0^{a}	0^{a}	0^{a}	$17^{a}\pm17.0$	$13^{a}\pm12.5$	$2^{a}+0.6$	0.0115
Bitternut hickory	1	0^{a}	0^{a}	tr^{a}	$4^{a}\pm2.9$	0^{a}	tr^{a}	0.192
(*Carya cordiformis*)	2	0^{a}	0^{a}	0^{a}	$1^{a}\pm0.6$	0^{a}	$2^{a}\pm0.6$	0.0155
Moonseed	1	0^{a}	0^{a}	0^{a}	0^{a}	tr^{a}	0^{a}	0.4389
(*Menispermum canadense*)	2	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	--

Appendix Table 2. Mean percent canopy cover ± Standard Error with SNK groupings and associated *p*-values. (Continued)

Floristics	TOPOGRAPHIC LOCATION							
	Hill	SRT	NRT	SMS	NMS	SLS	NLS	*p* value
Prickly ash	1	0[a]	0[a]	0[a]	0[a]	0[a]	1[a]±0.5	0.4389
(*Zanthoxylum americanum*)	2	0[a]	0[a]	0[a]	0[a]	1[a]±0.6	1[a]±0.6	0.096
Elm	1	0[a]	0[a]	0[a]	0[a]	0[a]	0[a]	--
(*Ulmus* spp)[c]	2	0[a]	0[a]	0[a]	0[a]	0[a]	4[a]±2.9	0.0492
Kentucky coffee tree	1	0[a]	0[a]	0[a]	0[a]	0[a]	3±3.0[a]	0.0573
(*Gymnocladus dioica*)	2	0[a]	0[a]	0[a]	0[a]	0[a]	0[a]	--
Bladdernut	1	0[a]	0[a]	0[a]	0[a]	0[a]	tr[a]	0.4389
(*Staphylea trifolia*)	2	0[a]	0[a]	0[a]	0[a]	0[a]	0[a]	--

[a] While most likely *Parthenocissus quinquefolia*, *Parthenocissus vitacea* may also be represented.

[b] While most likely *Symphoricarpos occidentalis*, *Symphoricarpos orbiculatus* may also be represented.

[c] Includes both *Ulmus americana*and *Ulmus rubra*.